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POST-FIRE REGENERATION OF WHITEBARK PINE: OBSERVATIONS OF SEED DISPERSAL BY CLARK'S NUTCRACKER

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INTRODUCTION

In the fall of 1989, whitebark pine (Pinus albicaulis) produced "moderate" to "good" cone crops in the Bitterroot National Forest, Montana, and Greater Yellowstone Area. The main purpose of this Cooperative Aid Agreement was to observe Clark's Nutcrackers (Nucifraga columbiana), the major dispersers of whitebark pine seeds, as they harvested and cached seeds in the vicinity of the Saddle Mountain Burn in the Bitterroot National Forest and in the vicinity of Mt. Washburn in Yellowstone National Park.

The Saddle Mountain burn represents an area in which whitebark pine regeneration is underway (see Final Report, June 1989, "Post-fire regeneration of whitebark pine: patterns of seedling establishment and nutcracker seed dispersal activity"). Whether nutcrackers continue to bury seeds in well-vegetated burned areas remains to be seen. In contrast, the whitebark pine communities in the Mt. Washburn area of Yellowstone National Park were severely burned in the 1988 North Fork Fire; thus, the cone crops of 1989 afforded the opportunity to observe whether nutcrackers are indeed attracted to recent burns for seed caching.

Specific questions concerning nutcracker seed caching behavior in both areas included how far nutcrackers travel from cone-bearing trees in the unburned forest to cache seeds in a burn (or elsewhere) and, what kinds of micro-sites they select for their seed caches.

An additional purpose of this Cooperative Aid Agreement was to survey possible study areas in the Greater Yellowstone Area for a long-term study of whitebark pine regeneration following the 1988 fires. This objective was accomplished.

PART 1. NUTCRACKER SEED HARVEST AND CACHING ACTIVITIES IN THE VICINITY OF THE SADDLE MOUNTAIN BURN

Study Area and Methods

The Saddle Mountain burn is located in the Bitterroot Mountains to the west and north of Lost Trail Pass. The burn resulted from a lightning-strike fire in 1960 that consumed about 1240 ha of forest and ranges in elevation from about 8400 ft at the top of Saddle Mountain to as low as 5400 ft at the extreme northwestern edge. The burn runs from the southwest to the northeast in its longest dimension. At the northeastern edge, the fire jumped across Hwy. 93, burning the adjacent, steep west-facing slope. Within the burn, the study area for the previous Cooperative Aid Agreement was a 3.2 km long section near the eastern edge, beginning near the unburned forest at the southwestern boundary. At the southern and southwestern perimeter of the burn is an expanse of unburned subalpine forest with both successional and climax stands of whitebark pine. A dirt road originating at the Lost Trail Pass ski area follows the ridgeline at the southwestern edge of the burn through the unburned forest to the top of Saddle Mountain. A number of dirt logging roads traverse the northeastern portion of the burn.

Nutcrackers were observed from 19 to 26 August, 1989 in the vicinity of the burn. Observations were made at several stops along the dirt road at the southwestern edge of the burn, including a viewpoint dubbed "cache flow", which is 1.7 k due south of the Saddle Mountain, and on Saddle Mountain. Additional observations

were made from logging roads near the clearcuts at the northeast edge of the burn and overlooking Hwy. 93. Time was also spent in the 1988 study area. Unfortunately, the weather was extremely poor during the field studies, with rain, fog, wind, and snow at the higher elevations; thus, the work was not as productive as hoped.

Summary of Results

The 1989 whitebark pine cone crop along the ridge to the southwest of the burn varied from stand to stand, ranging from "poor" to "good". On 21 August, few cones were damaged by nutcracker foraging. By 25 August, more cones per stand showed damage, although cone use was not uniformly distributed. For example, 8 trees bordering a meadow showed the following percentages of damaged cones out of total cones per tree: 89% (24/27), 0% (0/9), 6% (1/17), 17% (17/102), 0% (0/20), 67% (10/15), 9% (2/22), 0% (0/126). In addition, on 21 August, I observed as many as 5 nutcrackers at one time harvesting seeds from a very large whitebark pine with unusually abundant cone production. Every cone was damaged by nutcrackers. The above data, however, do not suggest a strong correlation between nutcracker activity and cone production per tree ($r = 0.10$, N.S.). Perhaps tree attractiveness depends on a combination of cone ripeness and productivity.

Nutcrackers were observed on several different occasions harvesting seeds from whitebark pine trees within sight of the dirt road along the ridge. In addition, nutcrackers were often observed flying overhead with full throat pouches. This behavior indicates that they were en route to seed caching areas.

An additional series of observations suggested that the subalpine forest south of the burn was a major source of whitebark pine seeds for nutcrackers and that nutcrackers were caching these seeds outside this area. Throughout the day there was a stream of nutcrackers with full throat pouches leaving from the south forest and heading in a northerly direction to caching areas. Nutcrackers, usually with deflated throat pouches, flew in from a northerly direction and headed into the unburned forest to the south.

Along the dirt road southwest of the burn is a low point in the ridge adjacent to elevation benchmark 7859 ft ("cache flow"). To the northeast of this low point is a valley between Saddle Mountain and the 1988 study area. Nutcrackers preferred this point on the ridge for their commuting. On 22 August, from 12:00 to 13:00, 16 birds flew north over "cache flow". Four of these had full throat pouches; the throat pouch condition of the others could not be verified. Nineteen birds, all with deflated pouches, flew south. This pattern was also observed from Saddle Mountain on 25 August from 13:00 to 15:00. During this period, 4 birds with full pouches flew north, 2 east, 1 south, and 2 west, whereas 13 birds with deflated pouches flew south and 4 flew west.

Observations from the logging roads on the northeast section of the burn indicated that few nutcrackers, if any, were caching seeds in the lower elevation areas of the burn. Nutcrackers with full throat pouches usually flew high in a predominatly northerly direction up the Bitterroot Valley. Their destination was not apparent. However, on 22 August at 17:30, one nutcracker with a full throat pouch landed on the steep, burned southwest-facing slope across Hwy. 93 and appeared to bury several caches.

The nutcrackers flying up valley were probably storing seeds for winter use in lower elevation slopes. On 26 August at 07:00, several nutcrackers were active on the slope behind the Sula Store. It is likely that they had stored seeds in the vicinity.

Although it was apparent that nutcrackers were not storing many seeds throughout the Saddle Mountain Burn, the birds were routinely storing seeds in selected locations in the higher, southwest parts of the burn. In the vicinity of the knob at the top of Saddle Mountain, nutcrackers with full throat pouches occasionally landed on the ground, strongly suggesting caching behavior. The steep, gravelly terrain on and around the knob is characteristic of sites preferred by nutcrackers for caching. On 25 August at 13:50, a nutcracker was clearly observed to make 5 or 6 caches of 3 to 5 seeds each in a north-facing slope across from the knob, fly into a tree, and then down to the ground to make additional caches. Steve Kroschel (pers. commun.) observed a nutcracker cache on the west-facing slope of the knob at 14:50 the same day, and we observed another bird cache on the same slope at 15:10.

Steve Kroschel, a cinematographer with Marty Stouffer Productions, contined his work in the area until 5 September. He reported (via letter) that nutcrackers tended to harvest and cache seeds in the vicinity of Saddle Mountain knob every evening, remaining in the last sunlit patches available in the area. On some evenings, as many as 6 nutcrackers would be caching at one time, while another dozen harvested seeds nearby or flew about. He estimated that most of the caching was done within a 3 to 5 acre area.

PART II. POST-FIRE WHITEBARK PINE SEED DISPERSAL BY CLARK'S NUTCRACKERS IN YELLOWSTONE NATIONAL PARK

Introduction

Clark's Nutcrackers (Nucifraga columbiana) are the primary disseminators of whitebark pine (Pinus albicaulis) seeds (Tomback 1978, Tomback 1982, Hutchins and Lanner 1982). These seeds are large and lack the woody seed wing typical of conifers; thus, the seeds cannot be dispersed by wind. When cones ripen, nutcrackers bury whitebark pine seed caches for use during other times of the year (Tomback 1978). Estimates suggest that a single nutcracker may store 32,000 to 98,000 whitebark pine seeds from one cone crop (Tomback 1982, Hutchins and Lanner 1982); seeds are typically buried under 1 to 3 cm of soil in clusters of 1 to 15 seeds, with a mean of 3 or 4 seeds (Tomback 1982), and are transported from a few meters to 12.5 km from parent trees to caching areas (Tomback 1982, Hutchins and Lanner 1982). Unretrieved caches may germinate, resulting in forest regeneration. Because whitebark pine is dispersed by birds, its seed shadow and population structure differ from those of wind-dispersed conifers (Furnier et al. 1987, Tomback et al. 1990, Tomback and Linhart 1990).

In the northern Rocky Mountains, whitebark pine forms climax communities on exposed sites and at timberline (Pfister et al. 1977). However, throughout most of the upper subalpine zone, whitebark pine is a pioneer that is slowly replaced by shade-tolerant conifers (Arno 1986, Arno and Hoff 1989). Historically, fires have initiated regeneration of whitebark pine in the northern Rocky Mountains at

intervals of 50 to 300 years (Arno 1980, Arno and Petersen 1983, Romme 1982). It has been assumed that nutcrackers are attracted to these recently burned forest tracts for seed caching, resulting in early regeneration of whitebark pine (e.g., Lanner and Vander Wall 1980, Arno 1986, Tomback et al. 1990). In fact, this assumption is the basis of a recent forest process model for whitebark pine (Keane et al. 1990a, Keane et al. 1990b). However, with the exception of one study in the Sierra Nevada (Tomback 1986), there has been no documentation of nutcrackers caching seeds in recent forest burns.

The 1988 fires in Yellowstone National Park were followed by an abundant whitebark pine cone crop in the late summer of 1989. This afforded an important opportunity to observe the seed dispersal activities of Clark's Nutcrackers in the vicinity of a severe subalpine forest burn, the result of the North Fork fire.

Study Area

The 1988 fires burned about 15% of the whitebark pine forest communities in Yellowstone National park (Kracht and Shovic 1990). Around Mt. Washburn, the subalpine forest, including seral and climax whitebark pine communities, was severely burned by the North Fork Fire, which began outside of the west park boundary (Yellowstone National Park 1989). The North Fork Fire burned 198,470 ha, by far covering the greatest area of the eight 1988 fires in the park (Greater Yellowstone Assessment Committee, 1988).

Mt. Washburn lies in the north-central part of the park, accessible from the road between Tower and Canyon Junctions. The elevation at the top of Mt. Washburn is 2700 m. Our observation

sites were along the trail from the picnic area on the southwest side of Mt. Washburn and pincipally along the north-south oriented ridgeline and burned forest on the northeast slope of Mt. Washburn, adjacent to the trail from Chittenden Road to the lookout at the top. The forest on the northeast slope was severely burned. All trees were reduced to charred snags, and the substrate was blackened and nearly devoid of vegetation with the exception of scattered clumps of fireweed (Epilobium angustifolium).

Bordering the ridgeline along the lookout trail are stands of cone-bearing whitebark pine that escaped the fire. Cone-bearing whitebark pine stands in the vicinity of Dunraven Pass and on the lower west slope of Mt. Washburn also escaped the fire.

Methods

We observed nutcrackers from 29 August to 1 September, 1989, for a total of 21 hours. Observations began as early as 09:30 and terminated as late as 18:00.

The number of seeds carried by nutcrackers during a caching trip was determined as follows. When a nutcracker first flew into a stand of whitebark pine trees and its sublingual pouch--the throat pouch used for transporting conifer seeds (Bock et al. 1973)--was deflated, each seed harvested by the bird and placed in the pouch was counted. In several cases, the count was terminated when the bird flew a distance to another tree; the count was successfully completed when the bird filled its pouch within observing range and flew off to cache. It is possible that one or two counts are under by a few

seeds.

When nutcrackers cached seeds in the burned forest below, we estimated the distance traveled into the burn from the edge to the nearest 10 m. Because nutcrackers remove from the sublingual pouch and cache one seed at a time, the number of seeds buried per cache could be observed in some cases; a few cache sizes may be undercounted. The direction in which birds flew to cache seeds from the ridge overlooking the northeast-facing burned forest was deduced by noting the directional flow of nutcrackers with full or empty throat pouches. We determined the hourly rate of nutcrackers flying out to cache and returning for seeds in the vicinity of the northeast aspect of Mt. Washburn from 13:45 to 14:45 on 31 August and from 10:50 to 11:50 and 14:00 to 15:00 on 1 September.

Standard deviations are reported with means.

Results and Discussion

Nutcrackers concentrated their foraging efforts in whitebark pine trees with both exceptionally large cone crops and cones already extensively damaged from previous foraging efforts. In contrast, other trees with many cones were hardly used; only a few cones per canopy were damaged by nutcrackers. This pattern of utilization suggests either asynchronous ripening of cones among trees (Tomback 1978) or more efficient seed harvest from cones already damaged. This latter makes sense, because whitebark pine cones do not open when ripe. Other species also harvested seeds from nutcracker damaged cones in the tree canopy, including chipmunks (Eutamias sp.), red squirrels (Tamiasciurus hudsonicus), Pine Grosbeaks (Pinicola

enucleator), and Cassin's Finches (Carpodacus cassinii). These species may rely on nutcrackers to open cones and facilitate their own foraging efforts.

We observed 12 nutcrackers fill their pouches from start to finish and fly off to cache seeds.; they carried from 28 to 97 seeds per pouchload ($\bar{x}$ = 53.9 ± 21.2). Tomback (1982) observed a range of 35 to 150 seeds per pouchload ($\bar{x}$ = 77 ± 37, n = 13). Hutchins and Lanner (1982) based their calculations of the number of whitebark pine seeds cached per individual nutcracker per year on full pouchloads (93 seeds), which some birds do not carry. Our observations suggest that 98,000 seeds stored per nutcracker is an overestimate.

Eight nutcrackers harvested a mean of 9.2 ± 3.6 seeds per min (range: 2.8 to 14 seeds per min). This is similar to Hutchins and Lanner's (1982) data for the same general time period. In 8 cases, single pouchloads of seeds came from one tree (i.e., trunk or genet), ranging from 28 to 97 seeds ($\bar{x}$ = 52.9 ± 23.1); this indicates that most of the seeds cached together were genetic relatives (see Tomback and Linhart 1990).

During one observation hour on 31 August, 26 nutcrackers headed north (NNW to NE) over the burned forest, starting from the ridge study area or south of the ridge. We could see full throat pouches on 20 of these birds but could not see the pouch condition of the other 6. Twelve of these birds flew down into the burned forest below us, landing from about 20 to 150 m below the upper edge of the burn. Those within about 50 m of the edge of the burn we could clearly see cache seeds. During the same hour, 17 birds, all with deflated throat pouches, returned from a northerly direction to the

ridge or flew south over the ridge.

On the morning of 1 September, we observed 16 nutcrackers fly in a northerly direction in one hour. We could see the throat pouches for 10 birds, which were carrying seeds, but not for the other birds. Four nutcrackers cached in the burn directly below us. Sixteen birds headed towards the ridge in the same hour; of the 14 we viewed clearly, none carried seeds. The pattern was similar during the afternoon viewing hour: 24 birds flew north, 15 confirmed with full neck pouches; and 16 flew south, 12 confirmed with deflated pouches.

This pattern suggested that many of the nutcrackers harvesting seeds in the vicinity of the north slope of Mt. Washburn were caching seeds in the burned forest below. The mean number of nutcrackers flying in a northerly direction, based on the 3 observation periods, was 22 per hour. If each bird were flying to a caching area and carried 54 seeds per pouchload, then nutcrackers originating their flights from this area were caching about 1200 seeds per hour, or about 150,000 seeds per day during daylight hours in the burned forest on the northern slopes of the mountain.

During the study, 17 nutcrackers wre observed to cache seeds at distances of about 0 m to 300 m from the edge of the burn. Eight of these birds cached seeds only a few meters inside the edge of the burn, and 5 could be observed clearly as they made 3 to 10 caches each. The number of seeds buried per cache could be counted for 4 nutcrackers (n = 23 caches): 1 to 15 seeds per cache, $\bar{x}$ = 5.2 ± 3.6 seeds per cache.

Seeds were buried in charred ground in all cases. Caches were buried in clumps of fireweed, in burnt forest litter, next to a fallen tree, within a clump of charred saplings, at the base of a

charred tree, and once at the edge near live krummholz whitebark pine trees and near grasses and sedges.

Nutcrackers were also observed to cache seeds in a steep, unburned south-facing slope on the west side of Mt. Washburn. Above the burn on the northeast slope, nutcrackers cached seeds on 5 occasions under the whitebark pine trees on the ridge or in nearby grass and forest litter. Two nutcrackers were observed to cache seeds in a north and east-facing slope at the parking area for Tower Falls, about 11 km NNE of Mt. Washburn. The source of their seeds was unknown.

In summary, nutcrackers appear to cache seeds readily in recently burned forest areas. By the summer of 1990, whitebark pine regeneration should be underway in the Greater Yellowstone Area. This is good news, because whitebark pine is now widely recognized as an important wildlife food source. Not only do a number of small mammals and birds feed on the large seeds (Tomback 1978, Smith and Balda 1979, Hutchins and Lanner 1982), but whitebark pine communities are designated critical grizzly bear (Ursus arctos) habitat (Craighead et al. 1982, Kendall 1983, Picton et al. 1986, Mace 1986).

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